MR STERLING B. TEBBETT (Orcid ID : 0000-0002-9372-7617)

MR ROBERT P. STREIT (Orcid ID : 0000-0002-3471-5878)

DR DAVID R. BELLWOOD (Orcid ID : 0000-0001-8911-1804)

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# A 3D perspective on sediment accumulation in algal turfs: implications of coral reef flattening

**Authors:**

Sterling B. Tebbett *, Robert P. Streit, David R. Bellwood

**Addresses:**

[1]ARC Centre of Excellence for Coral Reef Studies; and College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia

***Corresponding Author:**

Email: sterling.tebbett@my.jcu.edu.au

Phone: (07) 47815729

**Abstract**

1. Globally, coral reefs are being transformed by a suite of stressors, the foremost being climate change. Increasingly, it is expected that these reconfigured reef systems will emerge with lower-complexity and will be dominated by algal turfs. Understanding this new operating space is vital if we are to maintain the services, such as fishable biomass production, that reefs provide. However, the functionality of these systems appears to depend on the nature of the algal turfs themselves, which is in-turn, intimately linked to the sediments they contain.

2. As reefs are losing complexity, we need to understand if, and to what extent, algal turf condition and complex reef structure are connected. To address this issue we took advantage of recent developments in 3D structure-from-motion (SfM) technology to examine how complexity metrics (elevation and surface angle) related to the nature of algal turfs on a heavily climate-impacted coral reef. This represents a novel application of this technology in the context of coral reef ecosystems.

3. We found that as both elevation and surface angle decreased, the nutritional value of the epilithic algal matrix also decreased while sediment accumulation increased. Furthermore, we showed that elevated surfaces were characterised by far shorter algal turfs, and are potentially herbivory hotspots, offering fertile grounds for further exploration of herbivory dynamics at sub-metre spatial scales.

*4. Synthesis.* This study yields new insights into the operating-space of future reefs, and suggests that as reefs flatten, sediment accumulation is likely to increase even if sediment

inputs remain unchanged, altering algal turfs fundamentally. Maintaining key services provided by climate-transformed, low-complexity algal turf-dominated reefs of the future, will depend on managing the complex interactions between herbivory, sediments, algal turfs and reef structural complexity.

**Key words:**

Structural Complexity; Coral Reef; Cumulative Stressors; Herbivory; Photogrammetry; Epilithic Algal Matrix; Sediment; Climate Change

## Introduction

Coral reefs are amongst the most rapidly changing, hyperdiverse ecosystems on Earth (Barlow et al., 2018; Hughes et al., 2017). Repetitive, global coral bleaching events have challenged the status quo of these ecosystems (Hughes et al., 2018a; Wismer, Tebbett, Streit, & Bellwood, 2019). It is now critical to embrace these changes and understand how these transitioning ecosystems are functioning (Bellwood, Streit, Brandl, & Tebbett, 2019b; Graham, Cinner, Norström, & Nyström, 2014). This understanding is vital if we wish to support the desired ecosystem services that reefs provide (Bellwood et al., 2019a; Hughes et al., 2017). To understand future reef systems it will be critical to: a) identify the functional processes operating, and b) understand drivers of these processes.

The benthic configurations of future coral reefs is an area of ongoing uncertainty (Bellwood et al., 2019a; Bruno, Sweatman, Precht, Selig, & Schutte, 2009; Norström, Nyström, Lokrantz, & Folke, 2009; Smith et al., 2016). Predictions range from dominance by fleshy macroalgae (Mumby, Hastings, & Edwards, 2007; van de Leemput, Hughes, van Nes, & Scheffer, 2016), through boom-and-bust cycles of weedy growing corals (Berumen & Pratchett, 2006; Johns, Osborne, & Logan, 2014), to dominance by 'stress tolerant' coral taxa (Loya et al., 2001; Marshall & Baird, 2000). However, increasing evidence suggests that many reefs will emerge as low-complexity systems, dominated by turf algae (Arias-González et al., 2017; Bellwood et al., 2018; Jouffray et al., 2015; Smith et al., 2016). Low-complexity algal turf-dominated reefs seem particularly likely because: a) complexity on reefs is influenced by the three-dimensional skeletons of scleractinian corals (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Graham & Nash, 2013), which are increasingly susceptible to death and erosion during bleaching events (Hughes et al., 2018b; Perry & Alvarez-Filip,

2018), and b) algal turfs are often already the dominant benthic cover on coral reefs (Jouffray et al., 2015; Smith et al., 2016; Wismer, Hoey, & Bellwood, 2009). Furthermore, this coverage is set to increase in the future because turf algae can rapidly colonise dead reef substrata (Diaz-Pulido & McCook, 2002). Turfs are also particularly stress tolerant (Hay, 1981; Steneck, 1997) and even appear to benefit physiologically from future climate change scenarios (Johnson, Comeau, Lantz, & Smith, 2017; Ober, Diaz-Pulido, & Thornber, 2016). This proliferation of algal turfs per se may not be detrimental to the ecological functioning of reef systems, but may offer interesting new ecological configurations on reefs as turf algae are particularly productive and already underpin key trophic pathways on reefs (Hatcher, 1988; Kelly et al., 2017; Russ, 2003). As such, productive, turf-dominated systems, may have the potential to sustain key services, such as exploitable biomass production of fishes (Bellwood et al., 2018; Robinson et al., 2018).

However, the ability of algal turfs to sustain particular reef services appears to depend on the state of the algal turfs (Goatley, Bonaldo, Fox, & Bellwood, 2016; Tebbett, Bellwood, & Purcell, 2018). The state of algal turfs is, in-turn, intimately linked to the sediments they contain (Clausing et al., 2014; Goatley et al., 2016; Tebbett et al., 2018). By mediating key processes such as herbivory (Goatley et al., 2016; Tebbett, Goatley, & Bellwood, 2017b), coral settlement (Birrell, McCook, & Willis, 2005; Ricardo, Jones, Nordborg, & Negri, 2017; Speare, Duran, Miller, & Burkepile, 2019) and benthic productivity (Tebbett et al., 2018) sediments can mediate many critical processes of reef systems. This recent recognition of the ecological importance of turf-bound sediments appears timely, given that more than 50% of reefs are forecast to be at risk of increased terrestrial sediment inputs (Burke, Reytar, Spalding, & Perry, 2011). Indeed, declining water quality is considered one of the foremost stressors faced by coral reef systems, second only to climate change (Fabricius, 2005; Harborne, Rogers, Bozec, & Mumby, 2017; Jones, Bessell-browne, Fisher, Klonowski, & Slivkoff, 2016). We are therefore faced with low-complexity, algal turf-dominated reef configurations, whose critical process may be severely subdued by increased sediment inputs (Bainbridge et al., 2018; Tebbett et al., 2018). Yet, we know relatively little about important benthic dynamics in these systems, especially how reduced three-dimensional (3D) complexity affects the condition of algal turfs.

In coral reef ecosystems, complexity has received considerable attention, especially regarding its role in structuring the communities of reef-associated organisms (e.g. Emslie, Cheal, & Johns, 2014; Darling et al., 2017; Richardson, Graham, Pratchett, & Hoey, 2017).

In reef fishes, for example, the loss of structural complexity in particular, rather than the loss of coral cover per se, is expected to significantly alter the community composition (Emslie et al., 2014; Wilson, Graham, Pratchett, Jones, & Polunin, 2006). However, in terms of sediment dynamics, the effects of reduced structural complexity have received relatively little attention, especially regarding sediment dynamics related to algal turfs (but see Bodde, Pomeroy, van Dongeren, Lowe, & de Vries, 2014; Pomeroy et al. 2015; Torres-Garcia et al. 2018). The effects of complexity loss on sediment dynamics have the potential to be just as striking as those seen in fishes. This is because feeding by nominally herbivorous fishes plays a key role in redistributing and maintaining low sediment loads in algal turfs (Bellwood et al., 2018; Goatley & Bellwood, 2010) and this, in turn, appears to be mediated directly by structural complexity (Catano et al., 2016; Vergés, Vanderklift, Doropoulos, & Hyndes, 2011). Complexity, furthermore, mediates hydrodynamic activity (Lowe, Shavit, Falter, Koseff, & Monismith, 2008; Rogers et al., 2018), which in turn appears to impact algal turf sediment distributions on a range of spatial scales: from reef-wide distributions (Crossman, Choat, Clements, Hardy, & McConochie, 2001; Purcell & Bellwood, 2001; Tebbett, Goatley, & Bellwood, 2017a) down to the boundary layer created by algal turf filaments that enhances sedimentation rates (Carpenter & Williams, 1993). Evidently, a loss of structural complexity could affect biological as well as physical drivers of the distribution and retention of algal turf sediments across the entire reef system.

Understanding this relationship between structural complexity and the condition of algal turfs appears important if we wish to comprehend the functionality of low-complexity coral reefs of the future. A first step is to examine how complexity and the condition of algal turfs are intertwined. To address this knowledge gap we utilised recent developments in structure-from-motion (SfM) technology in combination with well-established algal turf sediment sampling on a heavily climate-impacted coral reef system. This represents the first application of SfM techniques to explore algal turf dynamics on reefs. This approach will allow new insights into the linking of sediments and complexity in a recently climate-reconfigured, algal turf-dominated system.

## Methods

*Study sites*

This study was conducted in Mermaid Cove (14°38′49.21″S, 145°27′16.34″E) at Lizard Island in the northern Great Barrier Reef (ESM Fig. S1) in January 2018. Lizard Island offered an exceptional system to study because it had undergone multiple, recent, largescale disturbances including back-to-back cyclones in 2014 and 2015 (Brandl, Emslie, Ceccarelli, & Richards, 2016; Khan, Goatley, Brandl, Tebbett, & Bellwood, 2017) and back-to-back coral bleaching in 2016 and 2017 (Wismer et al., 2019). Thus, the condition of this reef appears on-track to resembling future reef configurations. Within Mermaid Cove, three study sites were examined along the reef edge in the northern side of the cove (ESM Fig. S1). Each site covered 36 $m^2$ (6 × 6 m) and was delineated using transect tapes.

*Sediment sampling*

Within each site, 13 – 15 sampling locations were randomly designated. The benthic particulates (inorganic sediments and associated organic material) contained within the turfs at each of these random points was then sampled from within a 58 $cm^2$ PVC ring using a submersible electronic vacuum sampler (modified after Purcell, 1996). Suitable epilithic algal matrix (EAM)-covered areas for sampling were free of large sediment-retaining pits, macroalgae and encrusting organisms, and covered by turfing algae (following Tebbett et al., 2017b). Following particulate removal, within each sampling ring, 5 haphazardly selected algal turf filaments were measured using the depth probe of vernier callipers. To record this distance, the tips of the callipers were pushed into saltwater-resistant pressure-sensitive poster adhesive (blu tack). This distance was then measured using digital callipers following (Goatley & Bellwood, 2013). Algal turf length gives an indication of the ability of the turf to trap sediments, potential algal turf productivity and the intensity of grazing on algal turfs (Steneck, Mumby, MacDonald, Rasher, & Stoyle, 2018; Tebbett et al., 2018).

*3D photogrammetry*

Directly following the collection of particulate samples, the entire benthos at each site (36 $m^2$) was recorded using a Nikon Coolpix W300 camera by a diver swimming approximately 1.5 m above the reef following the methods described in Streit, Cumming and Bellwood (2019). This provided overlapping high-resolution imagery of the benthos, facilitating a photogrammetric reconstruction of the benthos using structure-from-motion software (Agisoft Photoscan Professional). This yielded orthorectified photomosaic maps, as well as 3D digital elevation models, of each site in sub-centimetre resolution (cf. Burns, Delparte, Gates, & Takabayashi, 2015; Figueira et al., 2015; Raoult, Reid-Anderson, Ferri, &

Williamson, 2017; Ferrari et al., 2018). The locations where particulates had been removed during the sediment sampling were clearly distinguishable on these photomosaic maps (see Fig. 1). Using the maps, we overlayed the digital elevation models and calculated surface elevation (relative to the lowest point at each study site) and surface angle (angle degrees from horizontal orientation), in 10 cm diameter rings, for each sediment sampling location at each site, in the software-package *raster* in the R statistics software (Hijmans, 2017; R Core Team, 2017). These two complexity parameters were selected because they were: a) meaningful in relation to coral reef flattening, and b) readily measured and intuitive. Detailed methods of the photogrammetric technique are provided in the electronic supplementary text (Text S1).

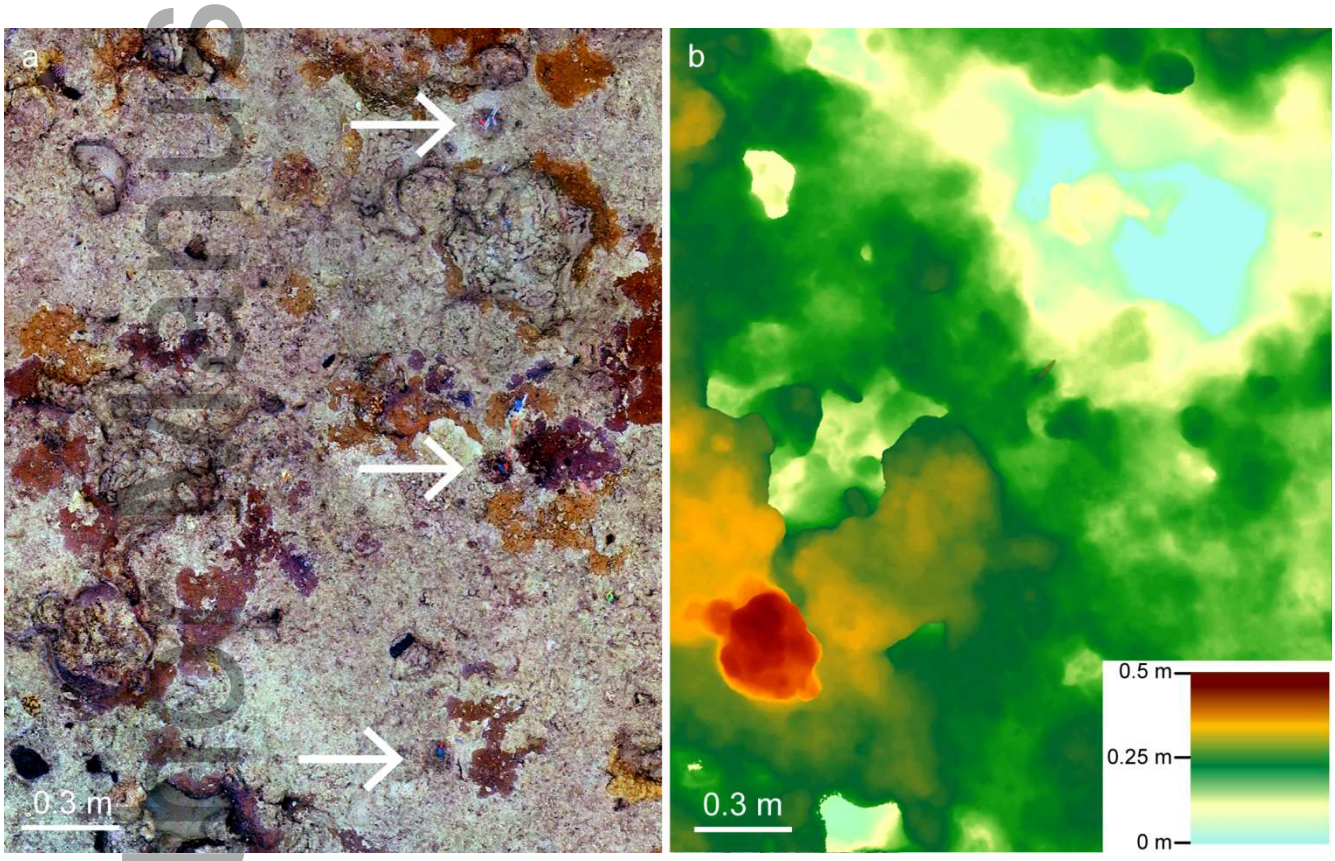


**Figure 1** a) Section of an orthomosaic map of the benthic cover at one study site (note the high coverage of algal turfs and the arrows indicating three locations cleared of sediments). b) The same location represented as a digital elevation model that was used to extract complexity metrics (the colour gradient indicates the highest elevation = red, lowest elevation = blue).

195 *Sediment sample processing*

196 To fix organic material in each particulate sample, 16 ml of 4% buffered
197 formaldehyde was initially added. Each sample was then transferred to an individual 9 l
198 container and left for 3 hours to allow particulate material > 10 µm to settle before decanting
199 the water (Purcell, 1996). Samples were then transferred to individual 120 ml samples jars.
200 Only particulate material < 2 mm (sands, silts and clays; ISO 14688-1:200) in each sample
201 was retained by wet sieving through a 2 mm stainless steel mesh. Each sample was then
202 agitated and allowed to settle for 24 hours (to ensure a consistent settling period) before the
203 depth of particulates in the sample jars was recorded at three haphazard locations around the
204 jar. To give the relative depth of particulates in algal turfs on the reef, measurements were
205 standardised by the sampling area.

206 Following depth measurements, salts were removed from each sample by rinsing with
207 fresh water three times, leaving a minimum 3 hour settling period between rinses. The
208 samples were then dried to a constant weight at 60˚C and weighed to yield total benthic
209 particulate mass. To remove organic material, samples were bleached for at least two weeks
210 using 30% hydrogen peroxide ($H_2O_2$) (following Gordon, Goatley, & Bellwood, 2016). The
211 samples were stirred and fresh $H_2O_2$ was added regularly. To yield inorganic sediment mass,
212 organic mass, and proportion of organics in benthic particulates the samples were then re-
213 dried and weighed, as above. Organic particulates (detritus) are a key trophic resource for
214 nominal herbivorous fishes (Wilson, Bellwood, Choat, & Furnas, 2003) and their relative
215 proportion to inorganic sediments is an indication of the nutritional quality of the EAM
216 (Purcell & Bellwood, 2001). Using a sieve stack (1000, 500, 250, 125, 63 µm) the bleached,
217 dried samples were then fractioned by particle size and the size fractions were individually
218 weighed.

219 *Statistical analysis*

220 A series of mixed effects models were used to examine how structural complexity
221 influenced six different components of the turf: (1) average algal turf length (mm); (2)
222 average benthic particulate depth in the algal turfs (mm); (3) benthic particulate mass (g $m^{-2}$),
223 i.e. the total mass of particulates in algal turfs; (4) inorganic sediment mass (g $m^{-2}$), i.e. the
224 non-nutritious component of particulates (Purcell & Bellwood, 2001); (5) organic detrital
225 particulate mass (g $m^{-2}$); and (6) proportion of organic detritus mass in the total particulate
226 mass (i.e. the relative nutritional value of all particulates as a whole).

Two complexity metrics (surface elevation and surface angle) extracted from the 3D models were considered as mean-centred explanatory variables. Multi-collinearity of the two explanatory variables was examined using correlation plots. In each model the explanatory variables were initially fitted as interacting fixed continuous effects, with subsequent model simplification based on the corrected Akaike's Information Criterion (AICc) (Table S1). All models also incorporated site as a random effect to account for the lack of spatial independence among samples. The model examining proportion of detritus in the particulates was based on a Beta distribution. In all other cases Gamma distributed, lognormal, and log-transformed models were considered, with final model selection based on residual plots and the fit of the model to the data (Table S1). Model assumptions were assessed using residual plots, all of which were satisfactory. All statistical modelling was performed in the software R (R Core Team, 2017) using the *lme4* (Bates, Maechler, Bolker, & Walker, 2015), *nlme* (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017), *glmmTMB* (Brooks et al., 2017), *AICcmodavg* (Mazerolle, 2017) and *ggplot2* (Wickham, 2009) packages.

The influence of the complexity metrics on the accumulation of different sediment grain size fractions was also explicitly examined. To do this, a distance-based linear model (DISTLM), was formulated, based on a Euclidian distance matrix of standardised grain size data. DISTLMs use multiple regression to find the combination of explanatory models that best explains the variation in sediment grain size distributions (Anderson, Gorley, & Clarke, 2008). Distance-based redundancy analysis (dbRDA) was then used to visualise the model. The DISTLM was performed in PRIMER 7.0 PERMANOVA+.

## Results

### *Turf components and complexity*

Our results revealed strong relationships between topographic complexity and the different turf components of the EAM (Fig. 2). The depth of benthic particulates, mass of benthic particulates, sediment mass and organic mass all exhibited similar patterns, showing significant decreases as elevation of the sampled surface increased (LME; $p < 0.05$ in all cases; Table S2; Figs. 2a, c, S2). Similarly, all four metrics decreased significantly as the angle of the sampled surface increased (LME; $p < 0.001$ in all cases; Table S2; Figs. 2b, d, S2). In no cases did the interaction between elevation and surface angle result in the most

parsimonious model (Table S1), i.e. an interaction between elevation and surface angle was not better at explaining any variation in the different turf component measures compared to each factor alone.

By contrast, the proportion of organics in the benthic particulates, and algal turf length, were related to complexity in a different manner. Inverse to the previous measurements, the proportion of organics in particulates significantly increased with both increasing elevation (GLMM; $p < 0.01$; Table S2; Fig. 2e) and increasing surface angle (GLMM; $p < 0.001$; Table S2; Fig. 2f). Algal turf length was only influenced by the elevation of the sampled surface; surface angle had no effect (Table S1; Fig. 2g, h). As elevation increased, algal turf length decreased significantly (GLMM; $p < 0.001$; Table S2; Fig. 2g).

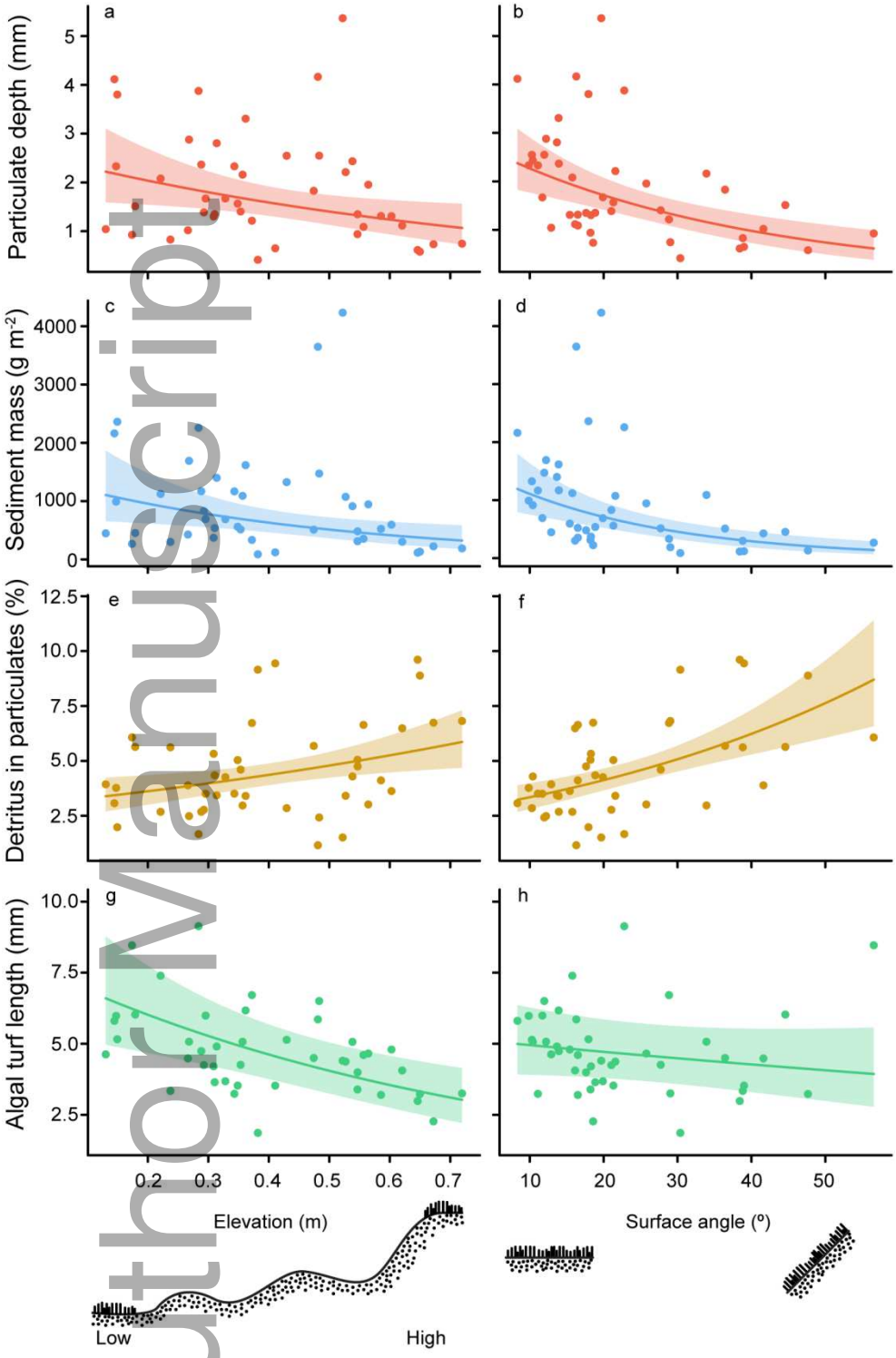


**Figure 2** The relationship between the elevation (a, c, e, g) and angle (b, d, f, h) of the sampled surface and components of the algal turfs, (a, b) particulate depth, (c, d) inorganic sediment mass, (e, f) the percentage of organic detritus (by mass) in benthic particulates, and (g, h) algal turf length. The lines mark the predicted fits from linear mixed effects models and their upper and lower 95% confidence interval, the points are the raw data points. For graphs

of benthic particulate mass and organic particulate mass see figure S2 in the supplementary material.

*Grain size distributions*

Elevation of the sampled surface was significantly correlated with the multivariate data cloud of sediment grain size distributions (DISTLM; pseudo $F = 11.79$, $p < 0.001$) which accounted for 21.9% of the total variation (Fig. 3). Silts and clays (sediment <63 µm), and, to a lesser extent, the intermediate 250 – 500 µm size class (medium sand), appeared to be positively associated with increasing elevation (Fig. 3). By contrast, coarse and very coarse sand (sediment 500 – 2000 µm) was negatively associated with increasing elevation (Fig. 3). In contrast to elevation, the angle of the surface was not significantly correlated with sediment grain size distributions (DISTLM; pseudo $F = 1.71$, $p = 0.17$), and only accounted for 3.9% of the variation.

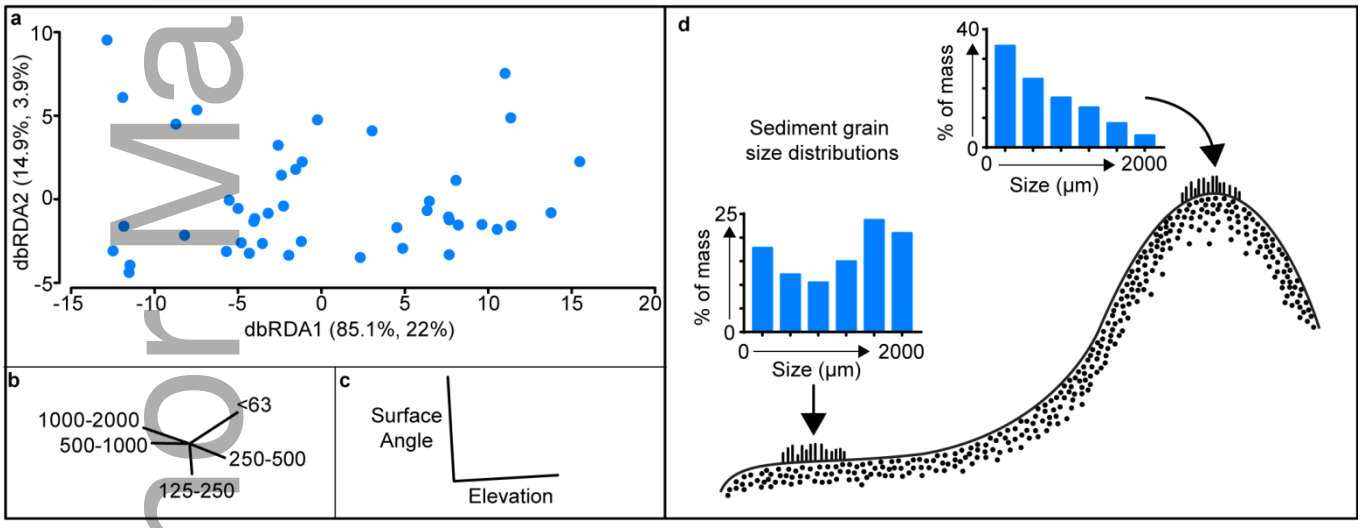


**Figure 3** a) a distance-based redundancy analysis (dbRDA) plot of the relationship between algal turf sediment grain size distributions and complexity (surface angle and elevation) based on a Euclidean distance matrix of standardised grain size distribution data (0 – 2000 µm). b) Vectors show the relationship among sediment grain size fractions (µm) and how they relate to c) the complexity metrics in the dbRDA plot. The 63 – 125 µm (very fine sand) vector did not contribute substantially to the observed patterns and is not shown. d) A conceptual diagram depicting the differences in grain size distribution at different elevations. Graphs of grain size distributions were based on the mean grain size distribution of 6 samples

representative of low and high points, respectively (i.e. located to the extreme left and right of the dbRDA plot).

## Discussion

Complexity in coral reef systems is expected to decline precipitously as corals, the architects of these ecosystems, are lost to repetitive largescale stressors (Alvarez-Filip et al., 2009; Graham et al., 2006). This loss of complexity is expected to have substantial ecological effects by restructuring the distribution, composition, abundance and interactions of reef organisms (Darling et al., 2017; Graham & Nash, 2013; Richardson et al., 2017; Wilson et al., 2006). We show that loss of complexity may also result in a reconfiguration of algal turfs. Since turfs are a dominant reef substratum that underpins fundamental reef processes such as benthic primary productivity (Bellwood et al., 2018; Hatcher, 1988; Klumpp & McKinnon, 1989), coral settlement (Arnold, Steneck, & Mumby, 2010; Birrell et al., 2005; Speare et al., 2019) and herbivory (Choat, Clements, & Robbins, 2002; Kelly et al., 2017), changing complexity could have far-reaching consequences for reefs.

While previous studies have suggested that microtopographic complexity is important in structuring the nature and photosynthetic abilities of algal turfs (Brandl & Bellwood, 2016; Carpenter & Williams, 1993), the role of topographic complexity at larger scales had remained relatively unexplored. The strong influence of complexity at the spatial scale assessed herein (cm – m) is likely to be a result of both hydrodynamic activity and the feeding activity of fishes. The effects of hydrodynamics are primarily revealed by the strong influence of elevation on sediment accumulation (Fig. 2). Elevated surfaces are more exposed to passing water currents, and wave activity, which limits the accumulation of sediments on such surfaces. Through mechanisms such as resuspension, or saltation, any sediments deposited on these elevated points are more likely to be dislodged and come to rest and accumulate in more protected, lower locations. This is particularly true for coarser sediments (Fig. 3). Similarly, in line with expectations, particulates also accumulated more on flat, low-angle surfaces where gravitational potential energy is minimised. Sediment accumulation on topographically-simple, flat locations appears intuitive and inevitable.

However, the accumulation of sediments is also likely to be driven by the feeding activities of nominally herbivorous fishes. These fishes interact with turf sediments in a

number of ways. Fishes can maintain low sediment loads through direct removal (e.g. scraping by parrotfishes [Bellwood, & Choat, 1990], or brushing by surgeonfishes [Goatley, & Bellwood, 2010]), or by maintaining short, cropped algal turfs minimizing their propensity to trap sediments (Goatley et al., 2016; Steneck, 1997). By contrast, if sediment loads get too high, sediments can directly reduce herbivory rates by mechanically protecting underlying algal filaments from removal or suppressing total fish feeding rates (Clausing et al., 2014; Eurich, Shomaker, Mccormick, & Jones, 2018; Fong, Bittick, & Fong, 2018; Goatley et al., 2016; Tebbett et al., 2017b). Additionally, high sediment loads can indirectly reduce herbivory, by lowering the nutritional value of the turf, through reduced turf productivity (Tebbett et al., 2018) or 'watering-down' relative levels of detritus in the particulate mixture (Purcell & Bellwood, 2001). More directly, fishes can also increase sediment in low laying areas through ingestion, transport and defecation (Bellwood, 1995), with parrotfishes defecating about 30 kg $m^{-2}$ $year^{-1}$ of sediment in the study area (Tebbett et al., 2017a). Hence herbivory by fishes drives, and is driven by, sediment loads in the algal turfs.

Compared to the relationship between sediments and complexity, algal turf length differed in that it was only negatively related to increasing elevation, but not surface angle. This relationship again appears to be underpinned by the interaction between herbivory and sediments (see Brandl, & Bellwood, 2016; Tebbett et al., 2017a; Duran et al., 2018). Most nominally herbivorous fishes feed predominantly on horizontal surfaces (Adam et al., 2018; Duran et al., 2018; Goatley et al., 2016), presumably because algal turfs on these surfaces are most abundant especially on reef flats, where they can have high productivity through exposure to light (Carpenter, 1985) or because this is where nutritionally important organic detritus accumulates (Crossman et al., 2001; Purcell & Bellwood, 2001) (Fig. 2). However, this is also where inorganic sediments accumulate when surfaces are not elevated (Fig. 2). As high sediments can reduce herbivory rates on turfs (Clausing et al., 2014; Goatley et al., 2016; Tebbett et al., 2017b), this is likely to explain why we could not detect a relationship between surface angle and algal turf length. Essentially on horizontal surfaces, algal turf length appears to vary substantially based on the elevation. Specifically, on horizontal, but elevated, surfaces, where sediments do not accumulate readily, herbivory is likely to be high leading to short turfs (see below). By contrast, on lower horizontal surfaces, that accumulate high sediment loads, herbivory is likely to be reduced, facilitating the growth of longer turfs. In essence, different algal turf states (short productive algal turfs [SPATs] and long sediment-laden algal turfs [LSATs] sensu Goatley et al., [2016]) are influenced heavily by reef

topography (Fig. 4). This highlights the potentially complex interactions between herbivorous fishes, reef complexity and the nature of turfs. It also offers fertile grounds for exploration of the heterogeneity of herbivory, and its links with turf composition, at small scales.

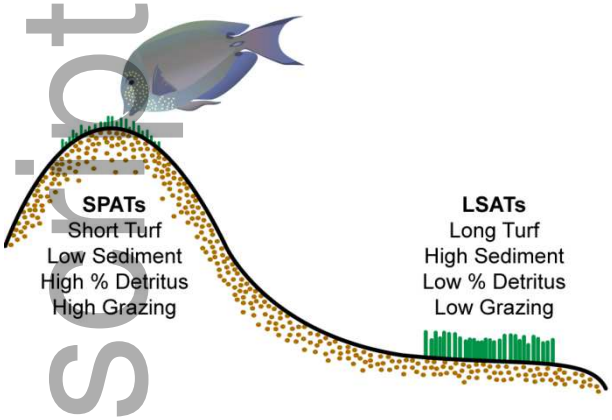


**Figure 4** A conceptual diagram showing the different nature of algal turfs at different elevations and the potential implications of this for grazing herbivorous fishes on reefs. SPATs = short productive algal turfs, LSATs = long sediment-laden algal turfs.

It must be noted that Lizard Island, where this study was conducted, has been heavily impacted by repetitive stressors (Brandl et al., 2016; Khan et al., 2017; Wismer et al., 2019) and appears to approach a future reef configuration. There has been a substantial loss of coral cover, likely resulting in losses of complexity (Madin et al., 2018; Wismer et al., 2019). While complexity had already been reduced at this location before our study, we still recorded up to 0.8 m of elevation between sampled surfaces; this level of elevation still had a clear effect on algal turfs and sediments. As heavily degraded reefs can approach 0 m of elevation (i.e. rugosity levels of 1) (Alvarez-Filip et al., 2009), there is likely to be further losses in complexity at Lizard Island, if reef recovery is delayed, promoting further sediment trapping in the algal turfs. Furthermore, as complexity was already reduced, the relationships between complexity and algal turf sediment dynamics described herein are likely to be conservative. On less impacted reefs, there is likely to be greater variation in complexity, and therefore, a larger magnitude of difference in algal turf sediments, potentially yielding stronger relationships. While the spatial scale of the current study was limited, our intuitive results support the results of other studies from other biogeographic locations (e.g. Duran et al., 2018), suggesting our general inferences would hold beyond Lizard Island.

Recently, evidence is emerging that fishes, particularly nominally herbivorous fishes, are far less dependent on complexity, especially that provided by corals, than often assumed

(Russ, Questel, Rizzari, & Alcala, 2015; Tootell & Steele, 2016). Indeed, it is becoming increasingly apparent that the nature and availability of nutritional resources may be far more important in structuring herbivorous fish communities than top-down factors (predation risk and shelter availability) (Russ et al., 2015; Tootell & Steele, 2016). However, our data suggests that fish herbivory, nutritional resource quality and complexity, are tightly intertwined. Elevated points are likely to receive the highest herbivory rates because they are less likely to accumulate sediments, have relatively high detrital levels, and are likely to be zones of high algal turf productivity (Fig. 4). Furthermore, these elevated points allow a greater field of view over the landscape when fishes feed, lowering predation risk (Bellwood et al., 2018; Brandl & Bellwood, 2015; González-Rivero et al., 2017). Therefore, elevated surfaces are likely to offer appealing feeding locations for herbivorous fishes, and this feeding activity could in-turn act to maintain low sediment loads in a positive feedback.

Essentially, the evidence suggests that turfs on flatter reefs can trap and retain more sediment, with LSATs prevailing. These LSATs are likely to be less productive with a lower nutritional value (Bellwood et al., 2018; Purcell & Bellwood, 2001; Tebbett et al., 2018). Such conditions have significant implications for the ability of these systems to sustain productive fisheries, especially in light of increasing sediment inputs onto coral reefs. Production of fishable biomass is one of the primary services provided by coral reefs to humanity, with many artisanal fisheries relying heavily on the herbivorous fish assemblage for this service (Edwards et al., 2014; Robinson et al., 2018; Russ et al., 2015). Unfortunately, heavy exploitation of herbivorous fishes often goes hand in hand with increased sediment inputs from terrestrial sources, due to land-clearing and agricultural practices (Burke et al., 2011; Hamilton et al., 2017; Seemann et al., 2014). Our findings highlight the importance of cumulative, anthropogenic burdens on reef systems: flatter reefs facilitate the trapping and retention of sediments in algal turfs, with potential flow-on effects on benthic productivity and harvestable fish productivity (Bellwood et al., 2018; Tebbett et al., 2018). Sustaining productive reefs in the face of these multifaceted interactions appears to be a particularly complex problem. Maintaining key services from future, low-complexity turf-dominated reefs, appears to be intimately linked to herbivory, sediments, complexity and the condition of the algal turfs.

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## Author Contributions

SBT, RPS and DRB conceived the study; SBT and RPS collected the data; SBT analysed the data and led the writing. All authors contributed critically to the drafts and gave final approval for publication.

## Data accessibility

Data is publicly available through the Tropical Data Hub, James Cook University, doi: 10.25903/5d0ada7f84903

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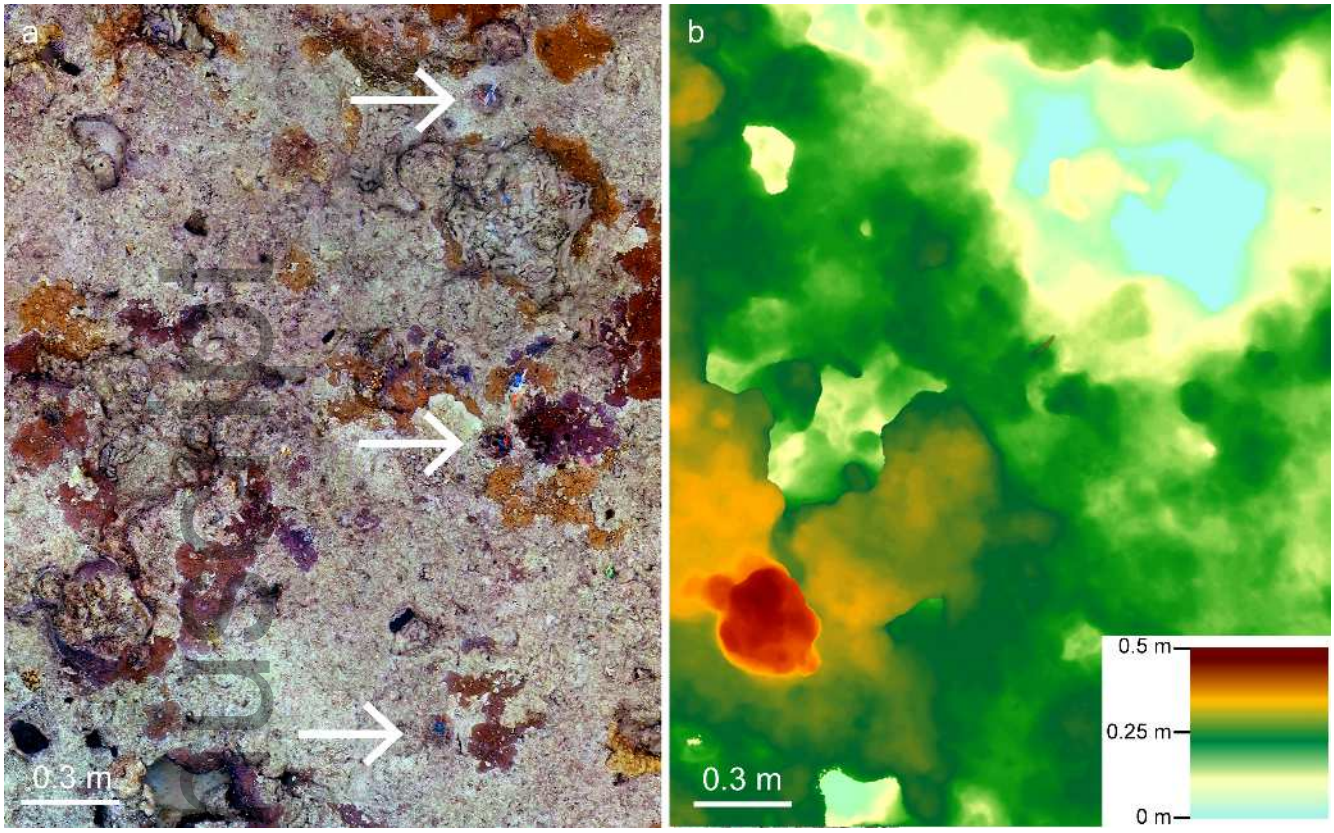


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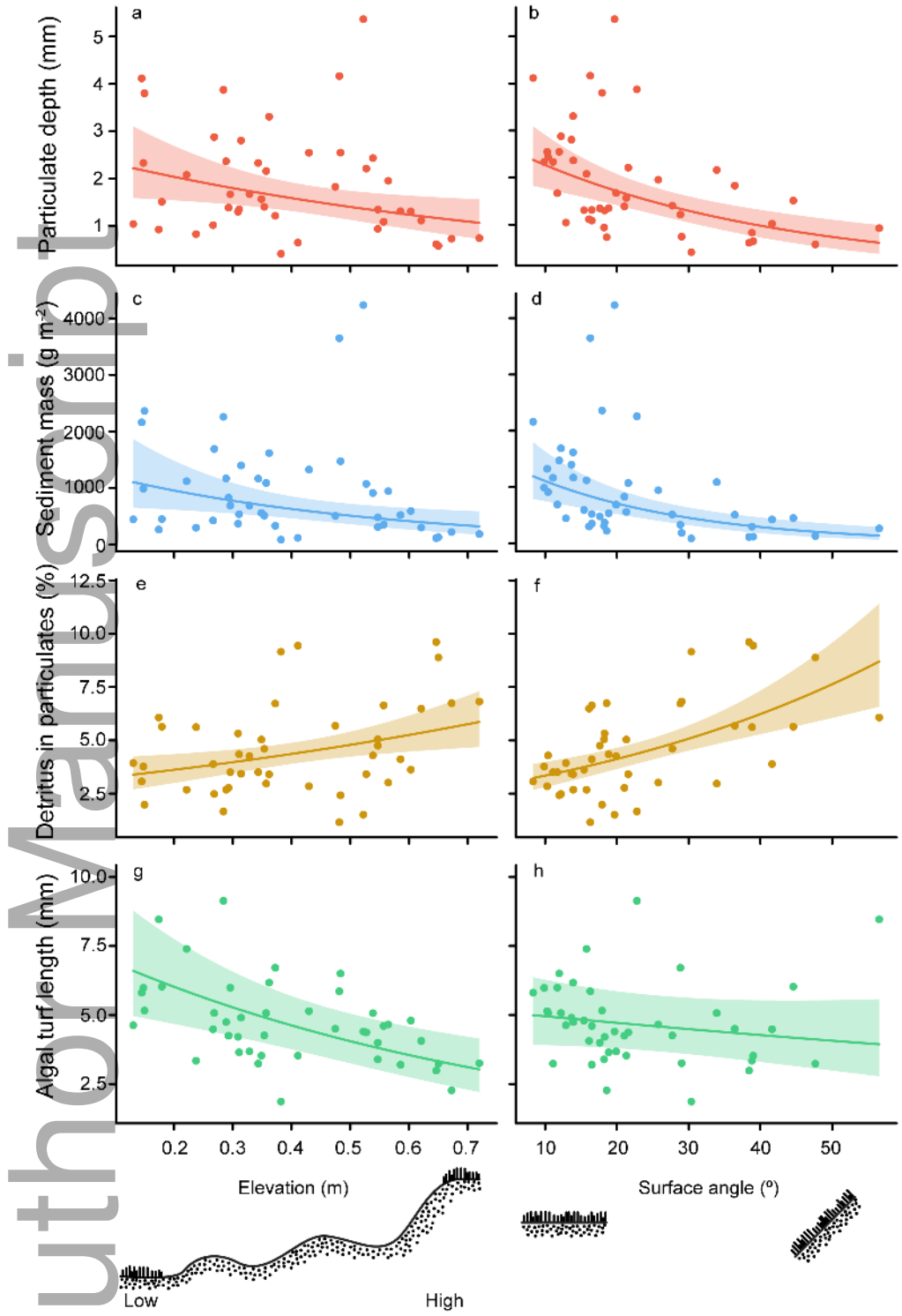


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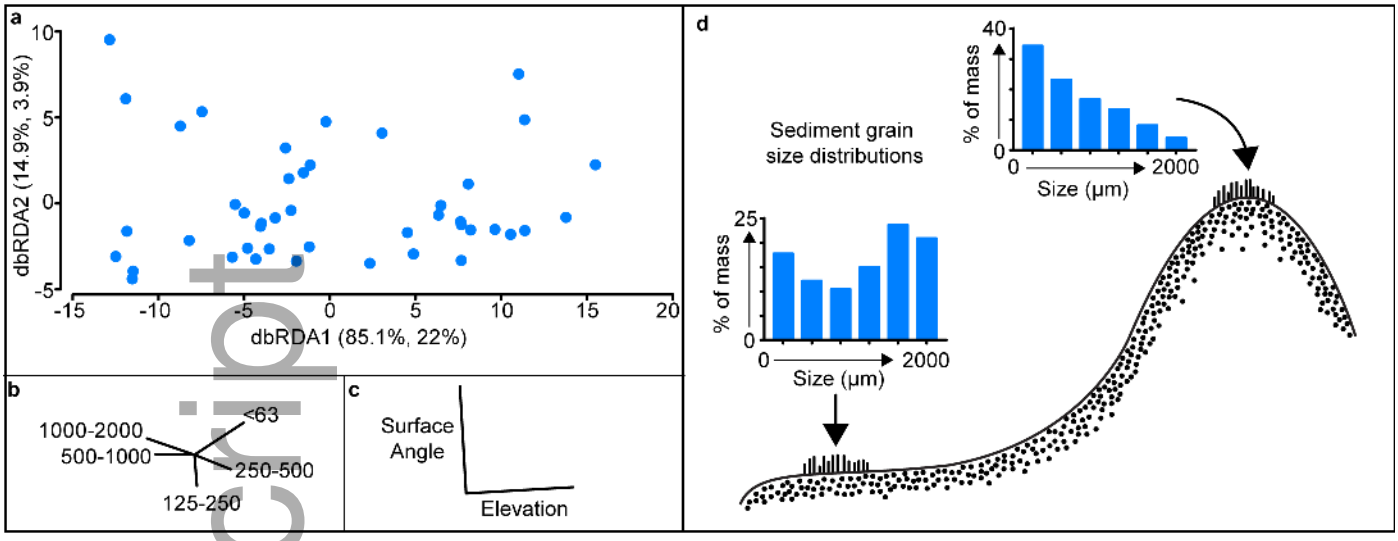


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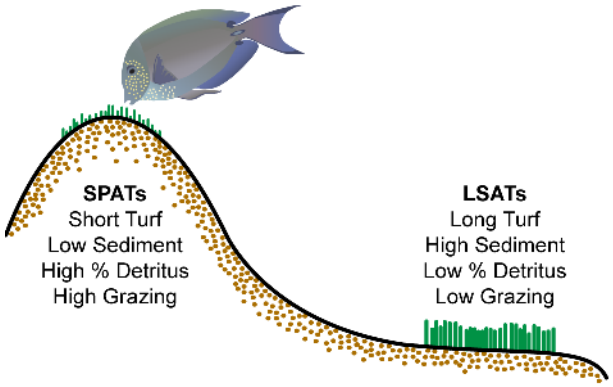


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